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European Odonata as hosts of *Forcipomyia paludis* (Diptera: Ceratopogonidae)

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Abstract

The biting midge *Forcipomyia (Pterobosca) paludis* is the only ceratopogonid species known to parasitise Odonata imagines in Europe. In this study, based mainly on the analysis of about 200 photographically documented cases, data on host species, parasite load and undisturbed position on the odonate body were analysed. The list of hitherto known hosts is extended significantly to include 55 Odonata species. The records date from mid-May to the beginning of August. Most data originate from southern France, Switzerland, Austria and Germany, with a few from Sweden and Croatia. Only females of *F. paludis* were found on Odonata, attached to both sides of the wings with a preference for their basal half, and mostly facing the wing base. In *Calopteryx* spp. the midges were likewise present on the wing tips. In a few cases midges were also found on the odonate's thorax and abdomen.

Introduction

The biting midge *Forcipomyia* (*Pterobosca*) *paludis* (Macfie) is a temporary ectoparasite of odonate imagines. Females of this small insect, only 1.8 mm in size, were found attached to their host's wings sucking haemolymph from the wing veins (Wildermuth & Martens 2007). However few records of *F. paludis* on odonates have hitherto been available (Macfie 1936a, b; Mayer 1936; Edwards 1937; Dell'Anna et al .1995; Clastrier et al. 1994; Szadziewski 1998). Being very inconspicuous the midges are often overlooked in the field and therefore often only detected when photographs or museum specimens of Odonata are analysed (e.g. Macfie 1932; Mayer 1936; Sternberg & Buchwald 1999: 166). In most cases the biting midges detach from their odonate host when they are captured in the insect net, beating their wings against the gauze or escaping through the mesh (Martens 1996: 72; Wildermuth & Martens 2007).

Some also fall from their dead host after collection. Since many aspects of parasitism of *F. paludis* on Odonata, such as seasonality, host range, parasite load and attachment site preferences on the host's body, were previously poorly known, we collected old and new data from various sources using different methods and present them here as a compilation. The major focus of this study was to determine the position of undisturbed biting midges on the odonate's body. Therefore, this work is mainly based on the analysis of photographs of odonate adults, a hitherto unusual source of data.

Methods

This study was based primarily on the analysis of our own and other odonatologists' general photographic records. Additional data were collected in the field by close inspection with the unaided eye or with close-focus binoculars, combined with some photographic documentation and selective collecting for species identification of the ceratopogonid. In the search for information we scoured relevant photographically illustrated odonate books on the general European or regional faunas

Figure 1: Distribution map of ceratopogonid midges recorded from European odonates. The size of the circles represents the number of records: 1-10 (smallest circle), 11-20, 20-50, >51 (largest circle).

(cf. Table 1). In several cases, an inquiry to the authors of published photographs resulted in additional material. In order to solicit further data, we presented our preliminary results on national and international odonatological congresses.

Due to the detachment and escape of many midges from netted odonates (Martens 1996: 72; Wildermuth & Martens 2007) data on captured individuals were excluded from quantitative analyses. As no ceratopogonid midge other than *Forcipomyia paludis* is known from Odonata adults in Europe so far (cf. references in the introduction), all data from Western and Central Europe were included into the analysis. The photographs were analysed with respect to date, locality, host species and sex, as well as the number and position of midges on the host's body. We payed special attention to the undisturbed position and orientation of the midges on the host's wings, i.e. upper and lower side of the wings, basal or distal half of the wings with respect to the nodus, fore and hind wing, orientation of the midge's body on the wing (cf. Fig. 2). For the analysis of phenology data, multiple records made by a recorder on the same day and at the same site were considered as one record. For host species, seasonality and geographical distribution, all previously published data were included in the analysis.

Figure 2: Female *Sympetrum depressiusculum* with four biting midges on the wings (circles). Two midges are attached to the under side of the wings (black circles) and therefore less distinctly visible than those on the upper side (white circles). Crau, southern France, 24 June 1993. Photo by AM.

Table 1. Records of European Odonata species with attached biting midges of cases based on photographs and literature. In four cases not tabled the host on the photo was not identified to the species level: *Coenagrion* sp. (1), *Platycnemis* sp. (1), *Orthetrum* sp. (2). N_{ph}: number of cases based on photographs.

Host species	N_{ph}	**Source**
Calopterygidae: *Calopteryx*		
haemorrhoidalis (Vander Linden)	4	GP; PP
splendens (Harris)	17	GP; PP; F. Petzold; Sandhall 1987: 29, 72
virgo (Linnaeus)	6	H. Kurmann; HE; Szadziewski 1998
Lestidae: *Lestes*		
sponsa (Hansemann)	2	C. Monnerat; HE; F. Petzold; Cowley 1936; Macfie 1936a, b
Sympecma		
fusca (Vander Linden)	-	F. Petzold; Clastrier et al. 1994
Coenagrionidae: *Ceriagrion*		
tenellum (de Villers)	4	B. Schneider; GP; Dell'Anna et al. 1995; GP in Sternberg & Buchwald 1999: 230
Coenagrion		
caerulescens (Fonscolombe)	1	PP
mercuriale (Chapentier)	17	GP; PP; A. Wiermann
ornatum (Selys)	3	GP; PP
puella (Linnaeus)	5	GP; PP; F. Petzold
pulchellum (Vander Linden)	1	B. Schneider; C. Monnerat; Macfie 1936a; Edwards 1937
Enallagma		
cyathigerum (Charpentier)	1	PP; F. Petzold; Edwards 1937
Erythromma		
lindenii (Selys)	5	GP; PP
viridulum (Charpentier)	2	J.M. Müller; PP
Ischnura		
elegans (Vander Linden)	11	B. Schneider; HE; GP; F. Petzold; Edwards 1937; P. Buchner in Raab et al. 2006
genei (Rambur)	-	Dell'Anna et al. 1995
pumilio (Charpentier)	1	HE
Nehalennia		
speciosa (Charpentier)	2	C. Monnerat
Pyrrhosoma		
nymphula (Sulzer)	1	GP
Platycnemididae: *Platycnemis*		
acutipennis Selys	12	GP; PP; A. Wiermann
latipes Rambur	8	GP; PP
pennipes (Pallas)	3	R. Bönisch; GP
Aeshnidae: *Aeshna*		
grandis (Linnaeus)	-	Michelmore 1929
isoceles (Müller)	2	A. Wiermann; AM; Mayer 1937; Dell'Anna et al. 1995; Sternberg & Buck 1994
Anax		
imperator Leach	1	HE
parthenope Selys	2	B. Schneider; AM

Boyeria		
irene (Fonscolombe)	1	GP; PP
Brachytron		
pratense (Müller)	-	Edwards 1937
Gomphidae: *Gomphus*		
flavipes (Charpentier)	1	J. Müller
pulchellus Selys	1	GP
simillimus Selys	7	K. Steiof; A. Wiermann; GP; PP
vulgatissimus (Linnaeus)	1	C. Monnerat
Onychogomphus		
forcipatus unguiculatus (Vander Linden)	1	A. Wiermann
uncatus (Charpentier)	12	K. Steiof; GP; PP
Cordulegastridae: *Cordulegaster*		
bidentata Selys	3	HW; HW in Meier 1989: 111
b. boltonii (Donovan)	5	HW; Wildermuth & Martens 2007
boltonii immaculifrons Selys	4	GP; HW
Corduliidae: *Cordulia*		
aenea (Linnaeus)	4	HW; F. Petzold; HW in Meier 1989: 109; HW in Sternberg & Buchwald 1999: 166; G. Lehmann in Landmann et al. 2005: 178; Wildermuth & Martens 2007
Oxygastra		
curtisii (Dale)	8	GP; PP; Gibbons 1986: 113
Somatochlora		
flavomaculata (Vander Linden)	2	HW; Mayer 1937
Libellulidae: *Crocothemis*		
erythraea (Brullé)	4	K. Steiof; AM; GP; PP; Dell'Anna et al.1995
Leucorrhinia		
albifrons (Burmeister)	-	F. Petzold
caudalis (Charpentier)	3	R. Bönisch; HE; K. Steiof in Kuhn & Burbach 1998: 194; HE in Raab et al. 2006
dubia (Vander Linden)	-	F. Petzold
pectoralis (Charpentier)	3	B. Schneider; HE (cf. Raab et al. 2006)
Libellula		
fulva Müller	5	AM; GP; PP
quadrimaculata Linnaeus	-	F. Petzold; Edwards 1937; Clastrier et al. 1994
Orthetrum		
albistylum (Selys)	1	HE
brunneum (Fonscolombe)	6	K. Steiof; A. Wiermann; GP; Sandhall 1987: 57
cancellatum (Linnaeus)	2	GP; Dell'Anna et al.1995
coerulescens anceps (Schneider)	1	R. Bönisch
c. coerulescens (Fabricius)	10	GP; PP
Sympetrum		
danae (Sulzer)	-	F. Petzold
depressiusculum (Selys)	1	AM; Martens 1996: 72
meridionale (Selys)	1	HE
sanguineum (Müller)	-	C. Monnerat
striolatum (Charpentier)	1	GP

Results

Altogether 22 European species of Zygoptera and 33 species of Anisoptera were found to host ceratopogonid midges (Table 1). All midges collected in France, Switzerland, Austria and Germany for identification proved to be females of *Forcipomyia paludis*. In total 202 photographic records of biting midges attached to Odonata provided analyzable data. The majority of the photos were taken in the Crau in Southern France (136 photos, 38 species). Further photographic records and additional data from observations originated from other regions of France and from Switzerland, Austria and Germany; Sweden and Croatia contributed single records (Fig. 1). About 70 observations incl. collecting from odonate wings were made at the Schwarzer See N of Fürstenberg, NE Germany (F. Petzold).

The seasonal records of midges on odonate wings are summarized in Figure 3. They dated from 17 May (year 2000, Burgenland/Austria, hosts: *Ischnura elegans* and *I. pumilio*) to 9 August (year 2005, Hinwil/Switzerland, host: *Cordulegaster boltonii*). A small dipteran on a wing of a male *Lestes viridis* (3 September 1995, Gut Sunder, N Germany, photo: GP) was excluded from the analysis because it could not be clearly identified as a ceratopogonid.

A total of 197 odonate individuals represented by photographs were analysed for number and position of the midges on their host, i.e. 91 Anisoptera, 27 *Calopteryx* and 79 other Zygoptera carrying a total of 468 ceratopogonid midges. Altogether 278 midges were found on Anisoptera, 57 on *Calopteryx* and 133 on other Zygoptera.

In most hosts the parasite load was low (Fig. 4), i.e. 60.8% of the infested individuals of Zygoptera (excl. *Calopteryx*, n = 79), 40.8% of the genus *Calopteryx* (n = 27) and 49.5% of the Anisoptera (n = 93) carried only one midge. In Zygoptera the maximum number of midges per host individual was seven, whereas Anisoptera reached 13 midges per host (Fig. 4).

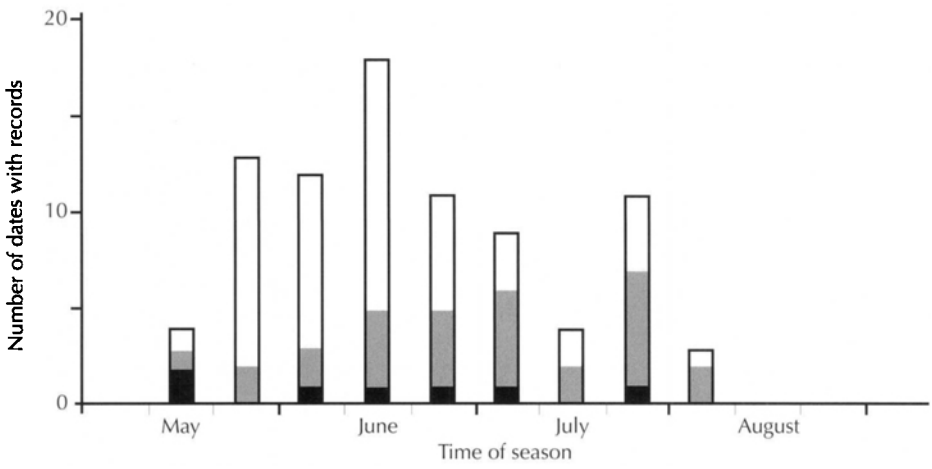

Figure 3: Phenology of ceratopogonid midges attached to odonate imagines in Europe. Pattern of the bars — ■: literature; ■: observation/collected material; □: photographic record.

Table 2. Orientation of ceratopogonid midges (n = 465) attached to the odonate wings.

Ceratopogonid midge	*n*	Frequency
Directed to the wing base	429	92.3
Directed to other directions	12	2.6
Not distinguishable	24	5.2

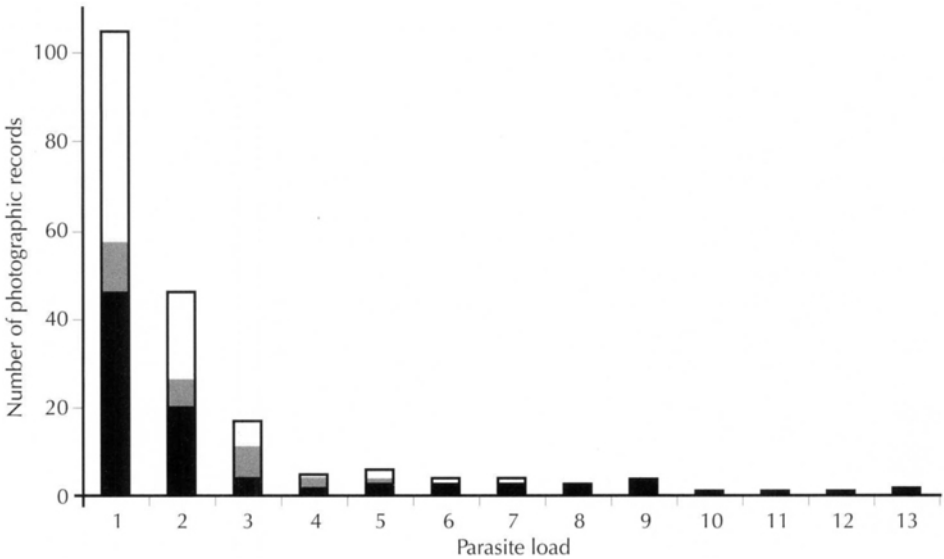

Figure 4: Frequency distribution of number of ceratopogonid midges per odonate host. Pattern of the bars — ■: Anisoptera; : *Calopteryx* spp.; □: other Zygoptera.

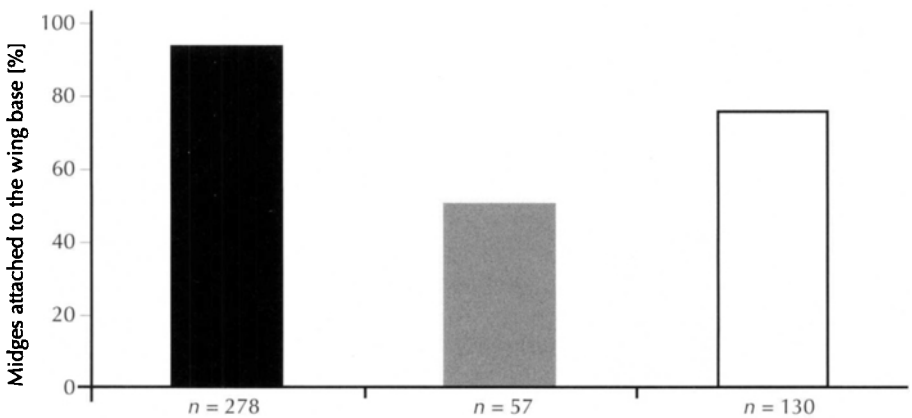

Figure 5: Proportion of ceratopogonid midges attached to the basal part of the wing (= proximal to nodus). Pattern of the bars — ■: Anisoptera; ■: *Calopteryx* spp.; □: other Zygoptera.

The majority of the midges (99.99%, $n = 468$) were attached to the host's wings. In Anisoptera, which have a smaller fore- than hind wing surface, the number of midges on the fore wings did not differ from that of the hind wings (134 midges on Fw, 144 on Hw; $\chi^2 = 0.36$, d.f. = 1, n.s.).

In Anisoptera most midges were attached to the basal half of the wing (261 vs 19). In Zygoptera (excl. *Calopteryx*) in which the basal wing area is much smaller than that of the distal part, the total number of midges on the distal part was significantly larger (100 vs 30; $\chi^2 = 15.23$, d.f. = 1, $p < 0.001$). In *Calopteryx* the portion of midges clinging to the distal half of the wings up to their tips (29 vs 28) was significantly higher than that of the other Zygoptera ($\chi^2 = 12.56$, d.f. = 1, $p < 0.001$; Fig. 5).

The extent to which midges were attached to the upper or under side of the wings differed between the suborders. In Anisoptera the midges were attached predominantly to the upper side (180 to the upper side vs 95 to the under side, two cases unidentified), whereas in Zygoptera (excluding *Calopteryx*) the midges clung more frequently to the under side (27 to the upper side vs 79 to the under side, 27 cases unidentified). The difference between the two suborders was significant ($\chi^2 > 28.78$, d.f. = 1, $p < 0.001$). In *Calopteryx* the position of the midges could often not be detected photographically, owing to being on the wrong side of an opaque wing in these insects. Therefore, all these cases were excluded from calculations.

On the wings most midges were orientated facing the wing base (Table 2). Four of 465 individuals were facing the wing tip, three faced towards the costa and one towards the hind edge of the wing.

Five midges were attached to other body parts than the wings. One freshly emerged male of *Cordulia aenea* bore a midge on the abdomen (May 1981, Hinwil/Switzerland, photo: HW). Two mature males of *Platycnemis acutipennis* carried one (29 May 1997, Crau/France, photo: GP) and two midges, respectively (26 May 1997, Crau/France, photo: PP) on the abdomen, and in a mature male *Coenagrion puella* one midge was attached to the thorax (28 May 1997, Crau/France, photo: PP).

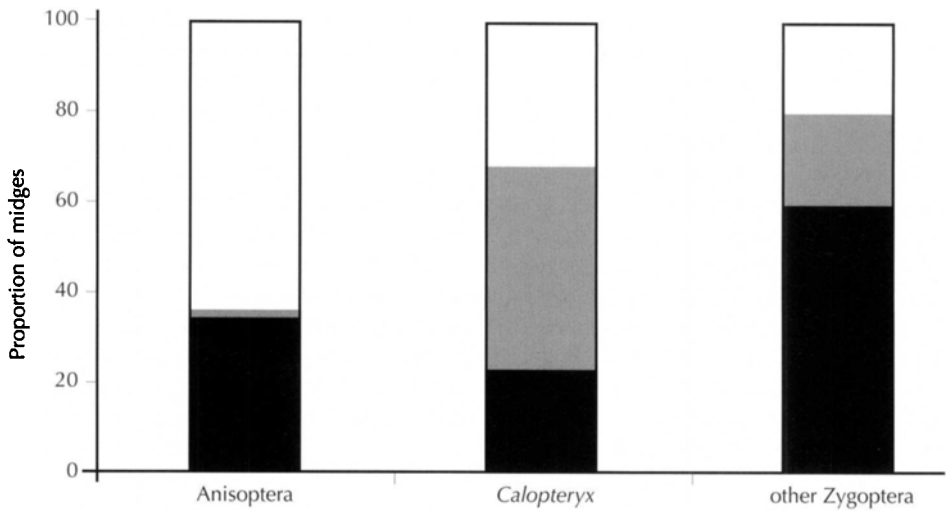

Figure 6: Proportion of ceratopogonid midges attached to the upper or under side of the odonate wings. Pattern of bars — □: upper side, ■: under side, ■: not distinguishable.

Discussion

In Europe altogether 55 odonate species are now documented with ceratopogonids attached to their body. So far, all midges identified to the species level belong to *Forcipomyia (Pterobosca) paludis*. It seems to be the only ceratopogonid species that attacks odonates in Europe. In other parts of the world a number of species is known from odonates within one region. In Japan, six species of biting midges are recorded from odonates (Naraoka 1999). Until Wildermuth & Martens (2007) described the feeding action it was doubted that the midges are true parasites. However, a phoretic association as supposed by Dell'Anna et al. (1995) may also occur. Therefore, photographs of attached midges alone do not provide definite evidence of parasitism. On the other hand, much other important information can be obtained from photographic records. Biting midges are recorded on nearly all odonate species with a flying season in spring and early summer. In Europe members of all odonate families are involved. It is concluded that *F. paludis* is not specific to any group within the odonates, and, because the species is not known from other insects so far, one can assume that it is host specific to the Odonata.

Besides biting midges other Diptera may be associated with odonate imagines. Sternberg (1993) described a milichiid fly, *Desmometopa* sp., acting as a commensal on an adult *Cordulegaster boltonii*. Flies moved from the thorax to the mouthparts of the dragonfly masticating a prey item. Yet, the second report on a supposed case of a commensal fly on a dragonfly's body (Sternberg & Buck 1994) should be reinterpreted as the photograph shows a ceratopogonid.

Up to now the database on *F. paludis* in Europe is too small to define the range of the species clearly. This biting midge is recorded from British odonates only in the beginning of its research history. All records are from the type locality, Wicken Fen, Cambridgeshire (Michelmore 1929; Cowley 1936; Macfie 1936a, b; Edwards 1937), but as far as we know, it has no longer been found there since. To our knowledge there is no record from the Iberian and Apennine peninsulas. The photograph of Sandhall (1987: 29) taken at the canal near Krankesjön, southern Sweden, seems to be the first record for Scandinavia. In the recent checklist (Szadziewski et al. 1997) the species is missing. *F. paludis* is recorded from Georgia by Remm (1967). These records base on free-living adults and include males, too. Additionally the species is listed for Romania (Remm 1988).

The recorded odonate individuals with ceratopogonids attached to their body belong to 22 Zygoptera and 33 Anisoptera species, respectively (Table 1). A comparison of these numbers with the total numbers of odonate species known from the range of *F. paludis* (Fig. 1; cf. Dijkstra & Lewington 2006: 36 Zygoptera spp., 63 Anisoptera spp.) reveals no significant difference in the relative portion of parasitised species between both groups (Zygoptera: 22 vs 14, Anisoptera: 33 vs 30; $\chi^2 = 0.002$, d.f. = 1, n.s.). Therewith no significant preference for any odonate taxon as host can be demonstrated for *F. paludis*. This is in contrast to *F. debenhamae* Cranston in Orr & Cranston that is recorded only from Zygoptera, and predominantly on *Libellago hyalina* (Selys) (Orr & Cranston 1997).

According to our findings parasitised Odonata were only observed between mid May and the beginning of August. The main flight season of Odonata in Central Europe lasts from the beginning of May until the end of September. This might help to understand why the majority of European species with an early flight season is

well represented and some common species with a late flight season such as *Aeshna cyanea* (Müller), *A. mixta* Latreille and *Sympetrum vulgatum* (Linnaeus) are missing from the host's list (Table 1).

F. paludis was almost exclusively found on the host's wings and only exceptionally on other body parts (cf. *Cordulia aenea* in Wildermuth & Martens 2007). This corresponds to nearly all findings of other ceratopogonids on non-European Odonata (e.g. Macfie 1932, 1936a, b; Cowley 1940; Naraoka 1999). However, *F. debenhamae* has been exclusively found on the thorax of hosts predominantly *L. hyalina* (Orr & Cranston 1997).

In the cases documented here, most odonate adults carried only small numbers of midges (Fig. 4). The parasite load of more than 170 midges attached to a teneral *Libellula quadrimaculata* as documented by Clastrier et al. (1994) seems to be highly exceptional. Anisoptera on average host higher numbers of midges than Zygoptera (Fig. 4). This might be explained by the larger wings of the former. However, the small and non-significant difference in parasite load between fore and hind wings in Anisoptera does not support this assumption. Perhaps the number of the midges is rather influenced by the absolute length of the main veins which may not differ in fore and hind wing significantly. The age of the host might also be important, with a possible preference for immatures (Dell'Anna et al. 1995), their cuticle being softer than in mature individuals.

In most odonate species the midges are predominantly attached to the basal half of the wing (Fig. 5). The proportion is especially high in the small and medium sized Zygoptera. In the case of the genus *Calopteryx* with coloured wings, this pattern deviates. We suggest that the high proportion of midges attached to the tip of the wings is related to the more intensive circulation of haemolymph in these dark coloured wing areas (Münchberg 1963) which is used to collect solar radiation (Rehfeldt 2005). A second but weaker argument might be the better stability of that wing area caused by dense venation.

In Anisoptera the biting midges were attached mainly to the upper side of their host's wings whereas in Zygoptera they colonized predominantly the under side (Fig. 6). We suppose that the midges attack their hosts while these are perching and these differences are caused by the suborder-related posture of the wings while perching. This may help to understand how and when ceratopogonids attach to the odonate's body. Most resting and perching Zygoptera hold their wings more or less above the back, the upper side of the wings facing and often touching each other. All European Anisoptera rest and perch with open wings, the under sides in some cases facing towards substrates. Presumably, the midges attack their hosts while in weather situations with hot and damp air as ceratopogonids are chiefly active in muggy weather (P. Havelka pers. comm.).

Most notably, the body axis in most midges that are attached to the host's wings is directed to the wing base. This is especially obvious in a photograph showing a rather teneral female *L. quadrimaculata* with ca 170 haemolymph sucking midges that are accumulated on the basal half of the wings (Clastrier et al. 1994; Grand & Boudot 2006: 74). We suppose that after landing on the wings the midges then crept towards the wing articulations in order to reach a position with the least possible mechanical burden caused by the centrifugal force, and air turbulence during the

host's flight. The latter is particularly suggested by the attachment to the clefts of the longitudinally folded wings (Wildermuth & Martens 2007), sites which might expect minimal turbulence during flight. However, more information is needed on the manner how biting midges attack their odonate host for testing these hypotheses. Furthermore, data are required as to a possible debilitating effect of *F. paludis* females on their hosts as has been demonstrated for *F. debenhamae* on *L. hyalina* (Orr & Cranston 1997).

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